Article

Genomic evidence of past and future climate-linked loss in a migratory Arctic fish

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Abstract

Despite widespread biodiversity losses, an understanding of how most taxa will respond to future climate change is lacking. Here we integrate genomics and environmental modelling to assess climate change responses in an ecologically and economically important Arctic species. Environmentally associated genomic diversity and machine learning are used to identify highly vulnerable populations of anadromous (migratory) Arctic charr, and we reconstruct estimates of effective population size spanning the twentieth century to identify past climate-associated declines. We uncover past region-wide declines in effective population size that correspond to decreases in temperature and community biomass in the Northwest Atlantic. We find vulnerable populations near the southern range limit, indicating northward shifts and a possible loss of commercially important life-history variation in response to climate change. The genomic approach used here to investigate climate change response identifies past and future declines that impact species persistence, ecosystem stability and food security in the Arctic.

Editor's Summary

Genomics and environmental modelling are integrated to assess past and future changes in Arctic charr populations ~~effective population sizes~~ in response to changing climate. Southern population vulnerability suggests climate change may lead to northward shifts and the loss of important life-history variation.

Main

Accelerated climate warming is profoundly altering marine and freshwater biodiversity, especially in northern regions with declining sea-ice cover[1, 2]. The downstream effects of warming include rising sea levels, changes to ocean circulation regimes and an increase in cold weather events in marine habitats[3, 4, 5], and increased precipitation and sedimentation in freshwater habitats[6, 7, 8, 9, 10]. Genetic adaptation can help buffer against rapid and continual environmental change[11, 12], and the evolutionary potential of a species may therefore determine its response to climate change[13]. Despite the importance of adaptive genetic variation, many studies do not consider local adaptation when predicting and elucidating species' response to future climate change[13]. Recent studies have begun to address this gap by utilizing genome-wide datasets to predict species' responses to climate change across a variety of taxa, by measuring 'genetic offset' or 'genomic vulnerability' (the magnitude of

mismatch between current and future genomic variation), the latter of which is modelled under current genotype–environment relationships[14, 15]. This method considers the genomic basis of adaptation and the complex relationship between adaptive diversity and the environment when measuring vulnerability. As such, it provides important insight into the evolutionary response to climate change, information that is lacking with only ecology~~y~~ical ~~-based~~ approaches. Previous studies have linked high genomic vulnerability to greater probability of decline[15], suggesting that declining populations lack the necessary genetic variation to adapt to rapidly changing environments. Given the link between the ability to adapt and vulnerability[13, 16, 17], protecting and sustaining biodiversity requires determining the genomic capacity for populations to respond to climate change.

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Forecasting climate change response is critical in Arctic species that provide essential economic and ecological services in an already vulnerable region[18]. For instance, migratory salmonid species support important northern fisheries, and their anadromous life cycle exposes them to climate impacts that integrate across both freshwater and marine habitats, increasing their vulnerability to decline[19, 20]. Arctic charr (*Salvelinus alpinus*), one of the most diverse vertebrate species[21], exhibits multiple life-history ecotypes across its Holarctic range (for example, ref. [22]). In the north, large migratory (anadromous) populations provide food security for local Indigenous communities, in contrast to the non-migratory (landlocked and resident) populations in the south, which are smaller in size and less often exploited[23]. The steep environmental gradients associated with this distribution make Arctic charr an ideal candidate for investigating genotype–environment relationships. Furthermore, a well-documented history of climate fluctuations in the North Atlantic Ocean (for example, refs. [24, 25]) provides a unique opportunity to investigate how this species has responded to past climate change. Though climate-linked declines in physiological condition of Arctic charr in the Canadian High Arctic have been suggested[26], uncertainty remains[27] regarding the magnitude of climate change response in this species and other Arctic fishes. Indeed, no study so far has used genomic data to investigate broad spatiotemporal species' responses to climate change in the Arctic, but recent work has called for these efforts[28].

Here we use genomic data and machine learning approaches to investigate spatiotemporal responses to climate change in an Arctic species by: (1) identifying the environmental variables correlated with spatial genetic variation along a steep gradient, (2) assessing genomic vulnerability to predict the potential response to future climate change and (3) identifying past climate-associated population declines. This Article reports climate-associated vulnerability and declines in an Arctic fish species with predicted shifts in life-history variation and impacts for ecosystem function and Indigenous food security.

Environment explains spatial genomic variation

We examined 16,431 ~~polymorphic~~ loci from an 87,000 single nucleotide polymorphism (SNP) array[29], 16,295 of which were polymorphic in anadromous populations studied here, to identify climate-associated genomic variation in Arctic charr. Although ascertainment bias is a concern with SNP arrays, the array used here was designed from a diverse suite of Arctic charr populations that includes individuals originating from the study region, and thus it is unlikely that ascertainment bias has ~~significantly~~ influenced the conclusions of this study. By sampling 744 individuals from 28 locations in northern Newfoundland and Labrador (Fig. 1a, Supplementary Table 1 and Supplementary Fig. 1), our study spanned steep environmental gradients, from dry tundra in the north (Fig. 1c) to wet boreal forest in the south (Fig. 1d). Our maximum-likelihood phylogenetic analysis mostly recovered clades as individual rivers (Fig. 1b), demonstrating substantial genetic diversity in this species, although some rivers showed regional-level structuring as has been previously demonstrated in Arctic charr[30]. Genetic differences among populations (linearized F_{ST}) correlated strongly with environmental differences (Euclidean distance of first principal component (PC1) explained 73% of the variance), demonstrating a strong signal of isolation by environment ($R^2 = 0.83$; Fig. 2a), even after controlling for geographic distance with a partial Mantel test ($R^2 = 0.43$, $P = 0.001$) (Supplementary Fig. 2). Next, to detect environment-associated SNPs, we ran a redundancy analysis (RDA) that included only uncorrelated environmental variables (Supplementary Tables 2 and 3), thus avoiding multicollinearity issues (Fig. 2b). Repeating the analysis with all 23 environmental variables collapsed into two PCs yielded an almost identical set of environment-associated SNPs (95.5% overlap; Supplementary Fig. 3), so we retain the use of uncorrelated variables for the remainder of the analysis. The RDA with five uncorrelated environmental variables (mean diurnal temperature range (BIO2), temperature annual range (BIO7), mean temperature of wettest quarter (BIO8), precipitation seasonality (BIO15) and optimal days; details

in Methods) identified 822 environment-associated SNPs on the first RDA axis and explained 10% of the spatial genomic variation ($P = 0.001$). These environment-associated SNPs were distributed across the genome, and they corresponded to SNPs that showed evidence of local selection, detected by pcadapt (Fig. 2c). The top environment-associated SNPs occurred near genes involved in protein modification (*TGOLN2*), growth factor activity (*TGFBR1*) and lipid metabolism (*COL18A1*, *ELOVL1* and *PITPNB*) (Extended Data Fig. 1). These types of process may play a key functional role in climate adaptation given evidence that links transforming growth factor signalling to circadian clock function in zebrafish (*Danio rerio*)[31] and changes in lipid metabolism in an Antarctic notothenioid (*Pagothenia borchgrevinki*)[32] to increasing temperatures. Environment-associated SNPs were significantly enriched for 85 gene ontology (GO) biological processes ($P < 0.05$, Supplementary Table 4), including immune and stress response, metabolism and growth, ion transport, oogenesis and reproduction, water and lipid homeostasis, and circadian rhythm. We then used a gradient forest machine learning approach to determine the most important environmental drivers of putatively adaptive genetic differences (environment-associated SNPs); we included all environmental variables here to compare their relative importance. The gradient forest identified maximum temperature of the warmest month (BIO5), average summer temperature ($AvgT_{Sum}$), mean temperature of the warmest quarter (BIO10) and precipitation of the driest quarter (BIO17) as key determinants of spatial genomic variation, consistent with findings in Atlantic salmon (*Salmo salar*) from the same region[33].

Fig. 1 I have uploaded a new version of this figure to the attachements that includes bootstrap values for the tree presented in part B. There have been no changes to the main text, only to the figure caption where I've now mentioned the presence of bootstrap values.

Steep environmental gradients and population structure in Arctic charr.

a, Sampling locations in Newfoundland and Labrador (Canada) numbered by decreasing latitude and overlaid on annual mean temperature (°C; BIO1) from WorldClim[63]. The black boxes represent the locations of the photos in **c** and **d**. Population codes can be found in Supplementary Table 1. **b**, Maximum-likelihood tree generated with 16,431 ~~polymorphic~~ SNPs. Populations have been collapsed into coloured triangles and numbers correspond to **a, and bootstrap values are shown at each node**. Most, but not all, rivers form monophyletic clades. **c**, A fjord in Torngat Mountains National Park in northern Labrador. Credit: S.J.D. **d**, Pinware River and surrounding boreal forest in southern Labrador. Credit: DASA images.

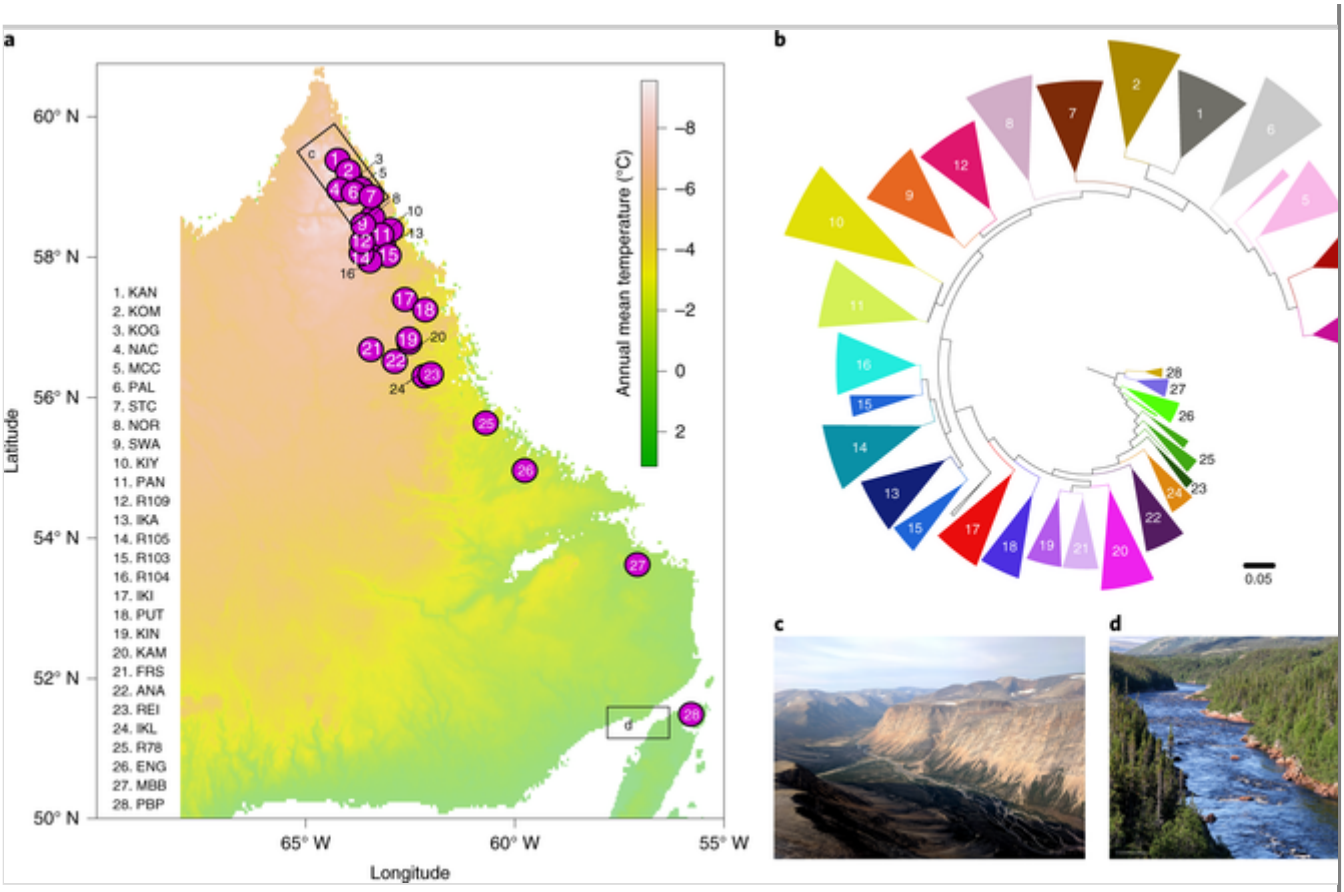

Fig. 2

Environment explains spatial genomic variation in Arctic charr.

a, Pairwise genetic distance (linearized F_{ST}) correlates positively with environmental distance. **b**, Five uncorrelated (R <~~>~~ 0.7) environmental variables explain 10% of genomic variation in an RDA. **c**, Environment-associated SNPs (green) highlighted across the genome correspond to loci that show evidence of local adaptation. Chromosomes are coloured in alternating grey and black. **d**, Gradient ~~random~~ forest-based feature selection shows that temperature, particularly summer temperature variables (BIO5, $AvgT_{Sum}$ and BIO10), explains spatial genomic variation in Arctic charr. Environmental variables corresponding to WorldClim codes can be found in Supplementary Table 2.

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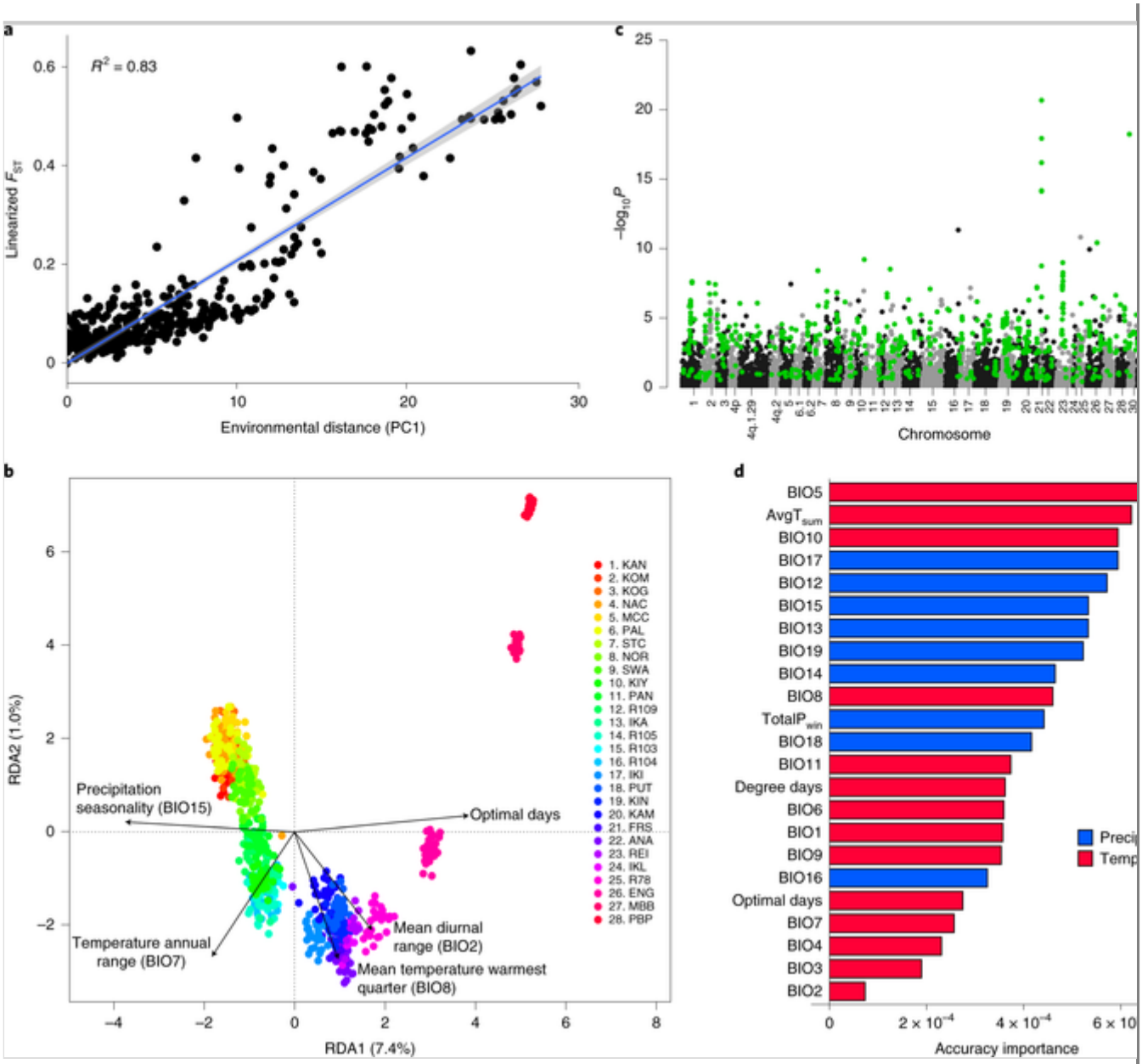

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Greatest vulnerability to climate change in the south

Previous studies have correlated genomic vulnerability, the magnitude of mismatch between current genetic variation and future environmental change, with probability of decline[15], offering a mechanism to link genetic diversity and climate change and ultimately identify those populations most vulnerable to future loss. However, this interpretation of genomic vulnerability makes several assumptions, including that the genetic data accurately reflect the genotype–environment relationship and that the environmental data and climate models are both spatially and temporally precise. Methods for calculating genomic vulnerability in this study follow refs. [14, 15], using a gradient forest model with minor allele frequencies (response) and uncorrelated environmental

variables from the RDA (predictors). Genomic vulnerability was highest in southern populations and correlated negatively with latitude (Fig. 3a–d) and nucleotide diversity (Extended Data Fig. 2 and Supplementary Table 5), consistent with an interpretation of reduced genetic diversity limiting the ability of southern populations to respond to environmental change[34, 35]. Genomic vulnerability also varied among emissions scenarios (representative concentration pathways (RCPs) 2.6–8.5), with higher emissions leading to increased overall vulnerability (Fig. 3a–d). Repeating the vulnerability analysis with a set of SNPs derived from a partial RDA, where the effect of a conditioning matrix (distance from most northerly site) is removed to account for geography, revealed similar patterns of vulnerability (Supplementary Fig. 4). Similar spatial patterns of vulnerability were also found using SNP signal intensities (Supplementary Fig. 5), which represent putative small-scale structural variants that could also be important in adaptation[36], suggesting that climate shapes multiple types of genomic variation in Arctic charr. To evaluate whether future environmental conditions for the anadromous populations in this study coincide with those regions where anadromy has been lost at the southern range limit, we performed a principal component analysis (PCA) with the top three environmental variables from our gradient forest model (Fig. 4). These results demonstrate that the future environmental conditions for our southernmost migratory populations are similar to current environmental conditions at sites where only non-migratory populations exist (Fig. 4).

Fig. 3

Genomic vulnerability is highest in southern populations.

a–d, Genomic vulnerability calculated with environment-associated SNPs based on projected environmental conditions in the year 2050 according to RCP2.6 (**a**), RCP4.5 (**b**), RCP6.0 (**c**) and RCP8.5 (**d**) emissions scenarios. We plot maximum temperature of the warmest month (BIO5; the top ranked variable in our original gradient forest model) across Newfoundland and Labrador and genomic vulnerability values for 28 populations in this study. Circle size and colour represent vulnerability, ranging from low (small, blue) to high (large, red). Inset: linear regression showing the negative relationship of Could you please remove 'of' here. between latitude and genomic vulnerability ~~is negatively correlated with latitude~~ under each emissions scenario. Grey shading represents confidence intervals around smoothed regression line.

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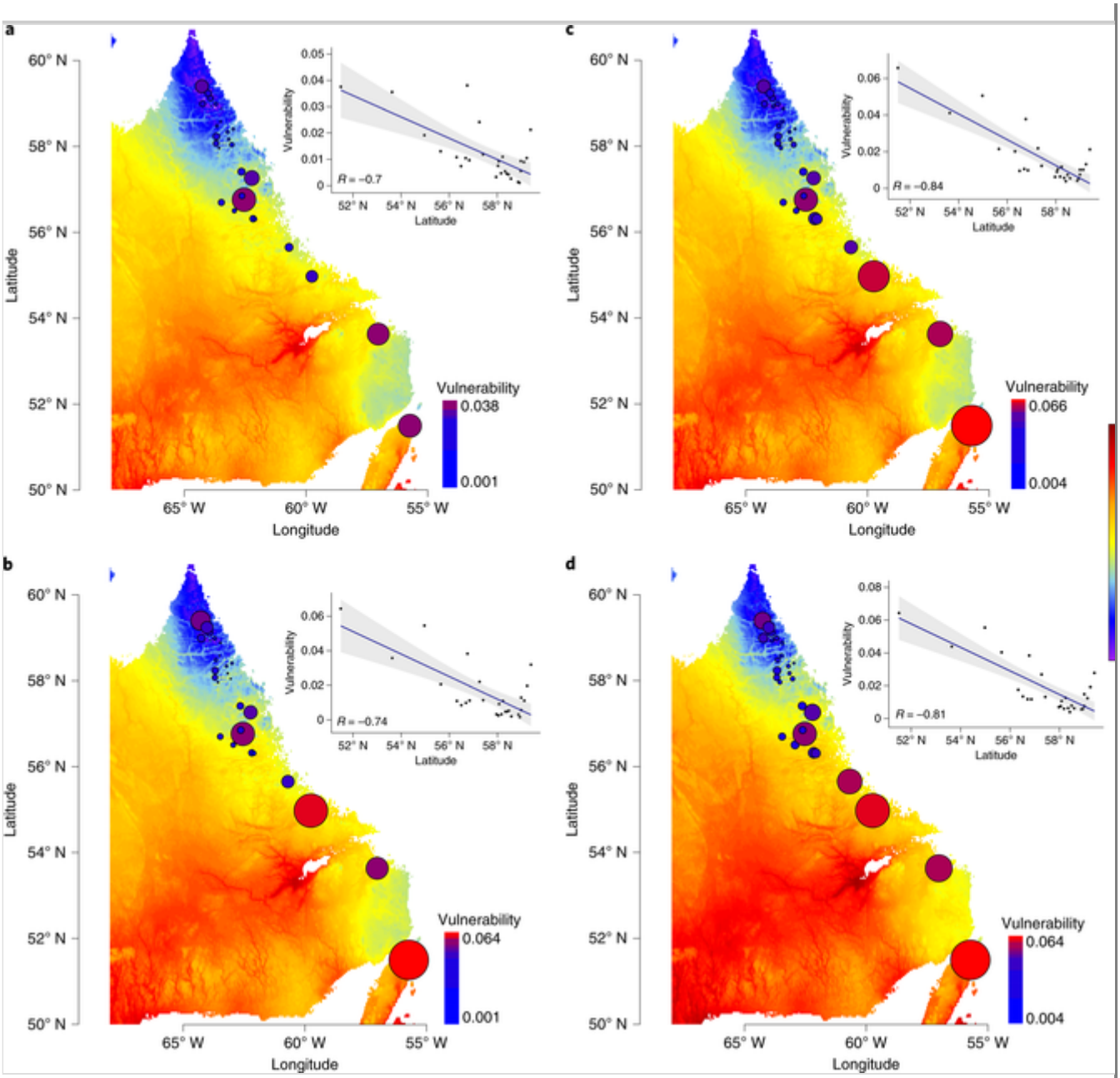

Fig. 4

Anadromous populations will be lost at southern locations.

A PCA with the top three variables from our gradient forest model showing that future environmental conditions for southern anadromous populations (red triangles) are more similar to current conditions in regions where anadromy has been lost (yellow squares) than where anadromy is present (blue circles). Larger symbols in ellipses represent centroids. Ovals represent group dispersion from the centroid (larger symbols). This statement should be removed. Anadromous populations in this study are labelled with locality codes (Supplementary Table 1) and non-migratory populations are labelled by state or province. The three populations at the southern end of the range appear in bold text. Inset: ridgeline plot from ggridges showing current and future values of maximum temperature of the warmest month (BIO5) at 28 locations in this study.

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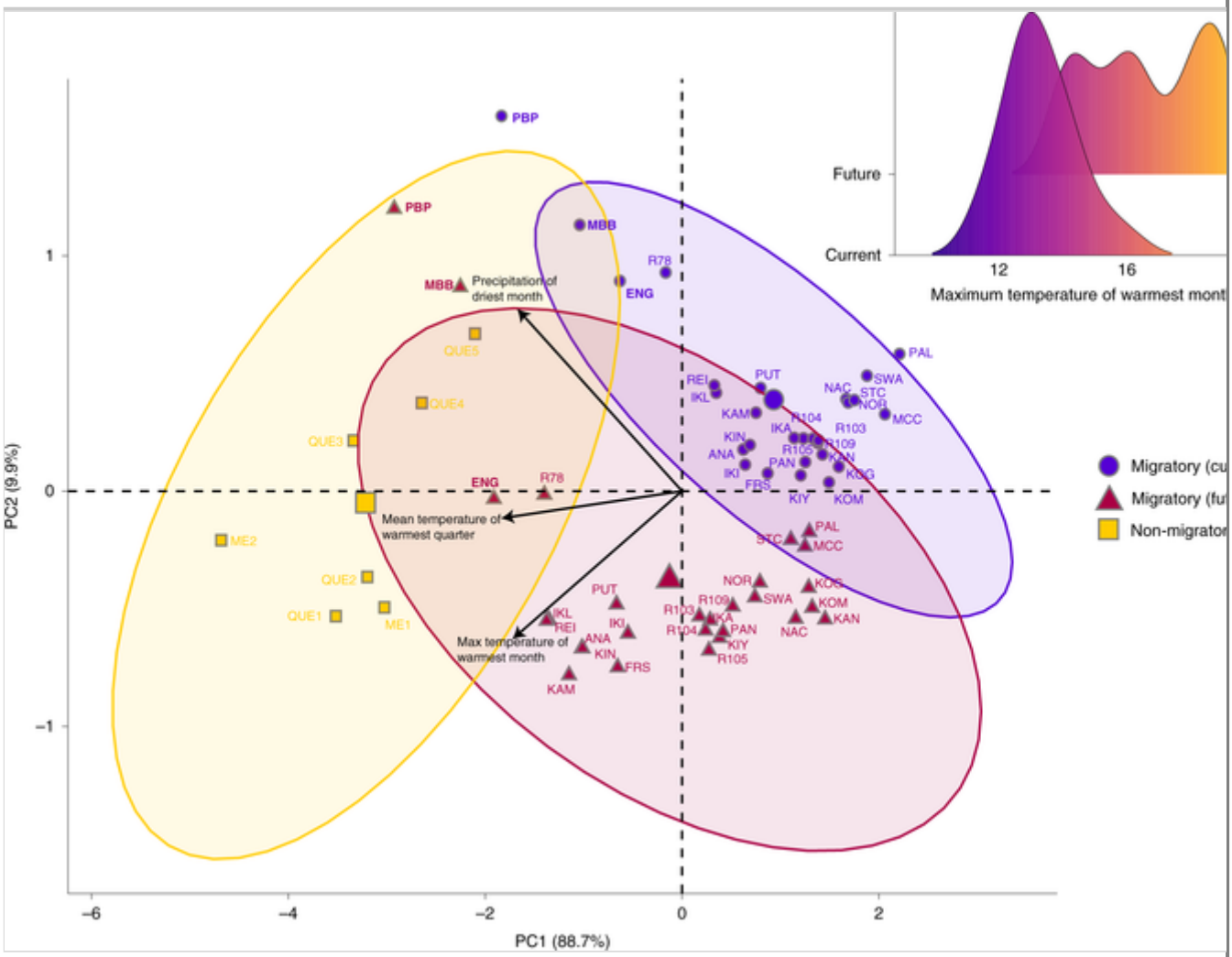

A past climate-induced decline in Arctic charr in Canada

To further evaluate whether vulnerable southern populations will experience detrimental impacts from future climate change, we investigated whether past declines coincided with shifts in climate. In the absence of estimated population trends for the region, we used multidecadal environmental data from the North Atlantic and reconstructions of effective population size (N_e), an evolutionary analogue to census size, to determine whether Arctic charr populations have previously declined in response to unfavourable climate conditions. We used the climate composite index (a sum of multiple environmental time series) and community biomass data (derived from 30 demersal fish species) from ref. [37], along with mean whole weight (kg) of Arctic charr, to investigate multidecadal temperature and biomass trends in the North Atlantic from 1985 to 2012. A decrease in the climate index in the early 1990s indicates cooler than average temperatures, with corresponding decreases in community biomass and mean

weight of Arctic charr during this time (Fig. 5a). In reconstructing N_e for 28 populations across four time points spanning 1900–2013 using the linkage-based method LinkNe[38], we observed a ~~significant~~ decline in N_e in all populations from the second (1990) to third (2001) time point, with a mean decline of 35.9% (range 32.1–48.8%; Fig. 5b), which may be a conservative estimate[38]. To quantify the loss of Arctic charr biomass during this time period, we examined the change in Arctic charr biomass (summed across 12 age classes) from the Nain region of Labrador before (1977–1984) and during (1990–1992) the decline that derived from Dempson 1993 and Dempson 1995 . Dempson 1993 and Dempson 1995 should be added to the reference list. See reference details in my response to query 22 below. Mean biomass during decline years was 39.3% (7.9–61.3%) lower than in pre-decline years, representing a ~~significant~~ substantial loss of Arctic charr protein to the surrounding community (Supplementary Table 6).

Fig. 5

Past Arctic charr populations have declined in response to climate fluctuation.

a, A decline in temperature (climate index), community biomass and mean whole weight (kg) of Arctic charr in the North Atlantic in the early 1990s. The black line represents the smoothed data relationship 'relationship' should be removed and the grey area represents the confidence interval around the smoothed line **b**, Region-wide declines in N_e (number of individuals) in Arctic charr track decreases in temperature, community biomass and weight. Inset: histogram showing that the total percent decline for each population varies from 30% to 50%. The dotted black box denotes the period of decline in both panels. The 95% confidence intervals for N_e estimates are provided in Extended Data Fig. 3.

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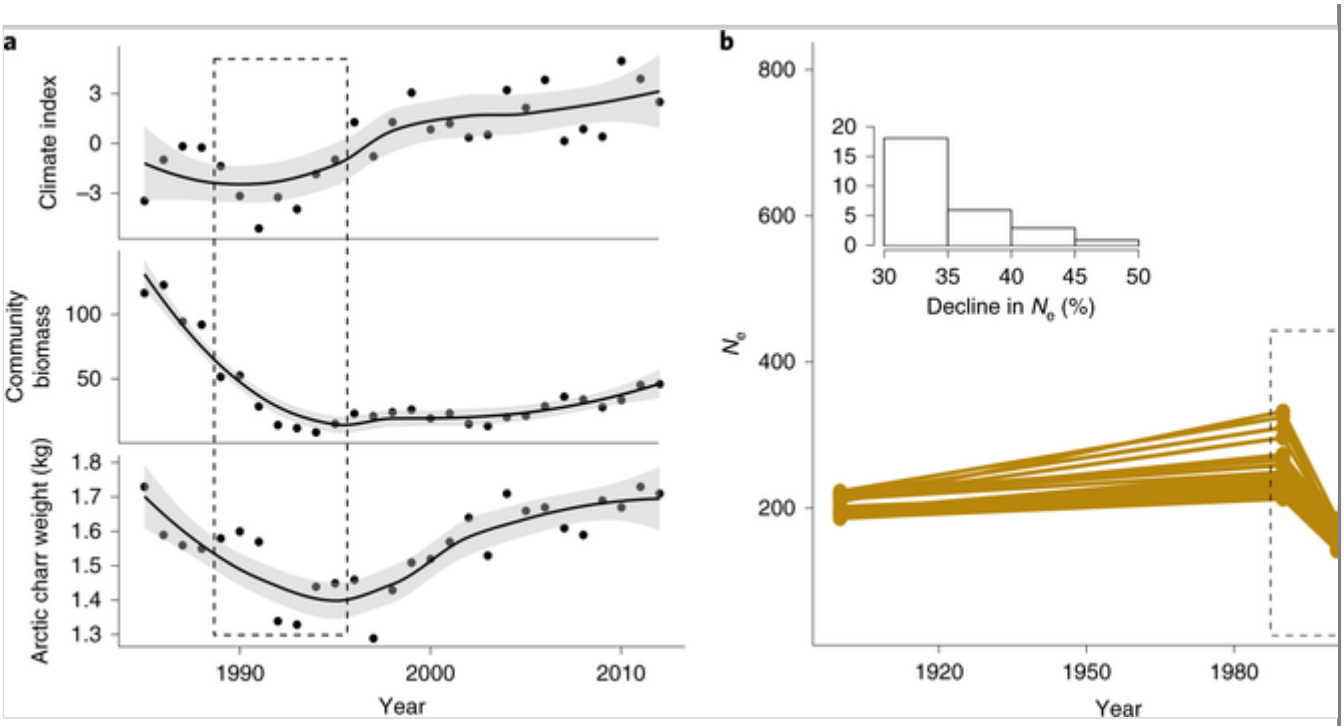

Discussion

Accelerated rates of climate warming in the Arctic threaten the persistence of species[39], and despite the importance of adaptive genetic variation in determining responses, predictions of climate change vulnerability often lack an evolutionary component. Here we use genomics, environmental modelling and machine learning approaches to document broad spatiotemporal responses to climate change in an economically and ecologically important Arctic species. Most notably, we found a gradient in ~~genetic diversity and~~ genomic vulnerability that declined with latitude, suggesting that anadromous populations at the southern range limit may be unable to adapt to pervasive warming in the Arctic. We also discovered a region-wide decline in the late twentieth century that corresponds to a period of unfavourable climatic conditions and documented regime shifts, reinforcing predictions that Arctic charr populations are influenced by climate. Our study uses evolutionary genomics to predict the impacts of future climate change and to identify past climate-linked declines in an Arctic species.

Biodiversity conservation in a changing climate necessitates identifying those populations most vulnerable to change. Given the role that genetic adaptation plays in structuring responses to environmental change[40, 41], studies can achieve greater predictive power and precision by integrating genomic data. High genomic vulnerability and low nucleotide diversity observed in populations in Newfoundland and southern Labrador in this study point towards a reduced adaptive capacity and evolutionary potential at the southern range limit (for example, ref. [42]). Range-edge effects probably contribute to the patterns of vulnerability and diversity observed here, given that these populations are fewer

in number, more isolated and restricted to areas with suboptimal habitat and conditions[43]. The vulnerability analysis used here is informative for linking genetic diversity and climate change, but it ~~does~~ assumes that the correlation among genetic and environmental data reflects the current genotype–environment relationship and does not necessarily provide insight into the mechanisms of adaptation ~~acting on this species~~. Nonetheless, given the current pace of climate change, combined with long generation times and low gene flow in Arctic charr[30, 44], we infer that vulnerable southern populations will be less capable of adapting to future environmental conditions without novel genetic variation[45].

The loss of the most southerly anadromous populations in Canada would represent a northward shift in the geographic range of this migratory ecotype. Existing evidence suggests that temperature limits the southern range of anadromous Arctic charr in the Northeast Atlantic[46], and our analysis suggests similar associations in the Northwest Atlantic with climate change probably inducing northward shifts in the distribution of anadromous populations. A projected increase in precipitation under future climate change scenarios is also expected to indirectly impact the occurrence of anadromy in Arctic charr, with increased terrestrial primary productivity bringing more nutrients to freshwater systems and reducing the propensity for migration[47]. Ultimately, the direct and indirect ecosystem impacts of the loss of southern anadromous populations probably extend to both abiotic and biotic processes, including changes in competition and predation dynamics. Previous studies have reported southern range contraction associated with loss of populations at warm latitudinal margins in northern birds[48] and plants[49], with more pronounced impacts anticipated at northern latitudes with higher rates of warming[50]. Our study predicts a range contraction of a single ecotype with the subsequent loss of life-history variation at southern locations, with similar climate-driven range contractions and loss of anadromy expected in Pacific coho salmon[51]. Because anadromous and resident Arctic charr occupy different niches ~~and the sole occurrence of the resident form is often associated with a loss of suitable habitat~~, and ~~because~~ fisheries in the region solely target the anadromous form, a shift from anadromy to residency at the southern range limit will result in a loss of diversity and productivity, even if this shift represents an adaptive response to climate change. The loss of populations at warm latitudinal margins can also induce a regime shift[52, 53] with downstream changes in ecological interactions[54] that have important implications for the stability of these ecosystems. Arctic charr also represent a critical resource for Indigenous communities[55] and the loss of anadromy at important fishing locations in the south, coupled with increased exploitation facilitated by Arctic ice melt[56], threatens the persistence and stability of this fishery and critical food source in Labrador. The potential

climate-associated loss of southern populations will directly inform joint fisheries management of the potential impacts to recreational, subsistence and commercial harvests, and presents an opportunity for genomic-based temporal monitoring of southern populations using targeted amplicons of climate-associated SNPs. Genomic data can improve the conservation status of this species by enabling more accurate delineation of conservation units and ensuring sustainable exploitation of these units, and it improves the accuracy of extinction risk models[57].

To determine whether Arctic charr exhibited past demographic response to climate, we assessed the potential for climate-induced declines by investigating past climate events in the region. ~~Significant d~~Declines in demersal fish community biomass in the North Atlantic in the early 1990s were partially associated with cold surface water temperatures (for example, ref. [58]), but population trends in Arctic charr during this time remained unclear before our study. The discovery of a past region-wide decline in Arctic charr in northeastern Canada that corresponds to this period of decreased temperature, community biomass and Arctic charr weight provides compelling evidence for the role of climate in this decline. The decreases in N_e observed in this study, coupled with the fact that genetic data covary with the environment, indicate that these are not simply plastic responses in behaviour and physiology. The linkage-based method used here to estimate trends in N_e combines estimates of recombination rate and linkage disequilibrium data and it has been used to reveal similar declines in Atlantic salmon[59] and Atlantic cod[60]. As such, this method has broad utility for exploring contemporary changes in population size across a diverse suite of taxa. Extreme climate events will continue to occur in the North Atlantic[61] and, when combined with continued increases in temperature at the southern range limit, will pose ~~significant~~ serious threats to vulnerable populations in this species. Although many populations in our study returned to, and in some cases, now exceed pre-decline numbers (based on N_e), the persistent effects of ongoing climate change will probably constrain genetic diversity and impact long-term recovery potential.

Our study provides an investigation of broad spatiotemporal responses to climate change in an economically and ecologically important Arctic fish, demonstrating highest vulnerability at warm latitudinal ranges and linking a past region-wide population decline to climate. The results presented here, and the climate-related decline of salmonids in the North Atlantic (for example, ref. [59]), strongly suggest the possibility of a southern range contraction and loss of anadromy under future climate change scenarios. Future work should look to extend our understanding of climate change response in the Arctic by identifying the mechanistic processes underlying this response, in line with recent calls for these

efforts[32]. This information will be particularly relevant for species that span the boreal–Arctic transition zone where pronounced climate impacts occur[62] and for species of conservation concern.

Methods

Sample collection and SNP genotyping

We collected 744 Arctic charr from a range of age classes for SNP genotyping from 28 rivers in northern Newfoundland and Labrador, Canada between 2005 and 2017 (Fig. 1a and Supplementary Table 1). Although sample collection spanned multiple years, this only reflects one or two Arctic charr generations and we detected no temporal pattern in the data that would impact population-based inferences (Supplementary Fig. 1). Similarly, family structure can also bias population-based inference, but previous examination of family structure using sequenced microsatellites has identified little evidence of siblings or half siblings[30]. The majority of specimens were collected with electrofishing, but fish counting fences and angling supplemented collections in southern locations. A Smith-Root LR-24 backpack electrofisher was used for electrofishing in shallow (<1 m) stretches of mainstems or tributaries. We preserved fin clips from fish in either 95% ethanol or RNAlater (Thermo Fisher Scientific), before extracting DNA using the Qiagen DNeasy 96 Blood and Tissue extraction kit following manufacturer's guidelines, and quantifying with either Qubit (Thermo Fisher Scientific) or Quan-tIT PicoGreen (Life Technologies). SNP genotyping used an 87,000 array following published methods[29], filtering for position on mapped chromosomes[64], minor allele frequency (0.01) and missing data (>0.05) in PLINK version 1.07 (ref. [65]) to yield a total of 16,431 ~~polymorphic~~ SNPs. We used all ~~polymorphic~~ SNPs for maximum-likelihood analysis in IQ-TREE version 1.6.8 (ref. [66]) with 1,000 ultrafast bootstrap replicates[67] and a general time reversible (GTR) model. Further statistical analyses were performed in the R programming language[68] (unless otherwise stated).

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Environmental data

We extracted a total of 19 current (1970–2000) and future (2050) environmental (temperature and precipitation) variables from WorldClim (resolution 2.5 arcmin) [63] Could you please verify that this reference is in the correct order? It comes after 64-68 in the previous section, but is cited first in the caption for Figure 1. using latitude and longitude with the bioclim package[69]. Extraction of future environmental variables utilized the Coupled Model Intercomparison Project Phase 5 data that incorporates 40 global climate projections across four different emissions

scenarios: RCP2.6, RCP4.5, RCP6.0 and RCP8.5. Some of the seminal studies in climate change genomics[14, 15] have also utilized these environmental data. Our study considered an additional four variables, including average summer temperature, total winter precipitation, degree days and optimal days. We extracted monthly average temperature and total precipitation from WorldClim (resolution 2.5 arcmin)[63] to calculate average summer temperature (June, July and August) and total winter precipitation (December, January, February and March). Extraction of daily temperature data from eight Environment and Climate Change Canada weather stations across Newfoundland and Labrador was done using the weathercan package[70]. To calculate cumulative degree days[71], representing midrange ambient thermal energy, we used the equation from ref. [71]. We assigned base temperature (T_0) a value of 0 °C as has been used for previous studies of Atlantic salmon from the same region[72, 73], and used minimum (T_{Min}) and maximum (T_{Max}) ambient temperature values from weather station data. We also calculated the number of optimal days, defined as the number of annual days with temperatures within an optimal range (10–12 °C) [74]. All 23 environmental variables were standardized before calculating genomic vulnerability. When calculating genomic vulnerability (see below), we omitted the number of optimal days and degree days because projected daily temperatures for 2050 are not available for deriving these values.

AQ18

Investigating environment-associated genomic variation

We used the genet.dist function in hierfstat[75] to calculate genetic differentiation among populations (F_{ST})[76] and then used linearized F_{ST} ($1 - F_{ST}/F_{ST}$) to investigate isolation by environment (IBE) and isolation by distance (IBD). Euclidean distance of PC1 from a PCA of all scaled environmental variables ($n = 23$) represented environmental distance. We calculated the least-cost distance between populations with the lc.dist function in marmap[77], representing geographic distance, and used a linear regression of linearized F_{ST} and both environmental and geographic distance to evaluate IBE and IBD, respectively. A partial Mantel test in vegan[78] determined the association between IBE and IBD.

We performed an RDA, a constrained ordination method with demonstrated low false positive rates relative to other methods for genotype–environment association[79], in vegan[78] to identify environment-associated loci. The RDA utilized 16,431 ~~polymorphic~~ SNPs from 28 populations and five uncorrelated environmental variables (BIO2, BIO7, BIO8, BIO15 and optimal days). It is worth noting here that large-effect loci may have gone undetected in this analysis given the low density of markers from across the genome. Correlations were

calculated with the stats version 3.6.2 package and we removed environmental variables that correlated strongly ($R > 0.7$) with more than one other variable. We chose a threshold value of 0.7 because it is standard in the field that this value represents a strong correlation[80] and this same threshold was used by ref. [15] to filter correlated variables in their study. In this case, the set of uncorrelated variables were not necessarily the most important in explaining genomic variation, but collinearity among variables can ~~significantly~~ influence the resulting genotype–environment patterns. The RDA was repeated twice, first with a conditioning matrix, distance from most northerly site (KAN), to partial out the effect of geography and second with all environmental variables collapsed into PCs. We identified climate-associated SNPs as those with loadings exceeding the 95th percentile on the first redundancy axis (RDA1), which explained latitudinal variation. To determine whether a scan for local adaptation also detected environment-associated SNPs, we used the pcadapt package with two principal components ($K = 2$) and a minor allele frequency cutoff of 0.01 to identify loci under putative selection[81]. We then mapped the RDA outliers onto a Manhattan plot. For our environment-associated SNPs, we conducted GO enrichment analysis using GO annotations in the *Salvelinus* sp. genome from ref. [82]. We extracted genes within 1,000 base pairs of the environment-associated SNPs and used topGO[83] to test for significant ($\alpha < 0.05$) over-representation of biological processes with a node size of five and the weight01 algorithm. To investigate the relative importance of environmental variables in explaining genomic variation, we ran a gradient forest model with 250 trees in gradientforest[84] using environment-associated loci and all 23 scaled environmental variables.

AQ19

Calculating genomic vulnerability

Methods for calculating genomic vulnerability follow ref. [15] and derive from ref. [14]. We built a second gradient forest model with 250 trees in gradientforest[84] using current, uncorrelated environmental variables (BIO2, BIO7, BIO8 and BIO15; predictors) and minor allele frequencies (response) to represent current genotype-by-environment relationships. Minor allele frequencies were calculated using genepopedit[85]. Using the gradient forest model, we transformed current and future environmental variables based on their importance in explaining genomic variation and calculated Euclidean distance between these current and future projected values. This distance represents genomic vulnerability, where greater magnitude difference between current and future projected values translates to higher vulnerability. We also investigated the relationship between genomic vulnerability and latitude for each emissions scenario and between genomic vulnerability and nucleotide diversity. Using

sliding windows of 10,000 base pairs in VCFtools version 0.1.17 (ref. [86]) we calculated nucleotide diversity both with all SNPs and with environment-associated SNPs and averaged across windows to derive a single value for each population. This analysis excluded population REI because of the small sample size. To determine whether future environmental conditions for the anadromous populations in this study match those at locations where anadromy has been lost[87] (Supplementary Table 1), we performed a PCA with the top three environmental variables from our gradient forest model and plotted this with the factoextra package.

We extracted signal intensity data for environment-associated SNPs from raw CEL files using the PennCNV-Affy (Axiom array) pipeline[88]. Briefly, this pipeline generates genotype calls from raw CEL files, extracts allele-specific signals, and generates a canonical genotyping clustering file that is used to calculate log *R* ratio (LRR) values, representing signal intensity. We ran an RDA using LRR values for 13,663 sites from 28 populations and five uncorrelated environmental variables ($R < 0.70$) (BIO2, BIO7, BIO8, BIO15 and optimal days) to identify environment-associated sites. These environment-associated sites were then used as response variables (rather than allele frequencies) for calculating genomic vulnerability. Differences in signal intensities represent potential copy number variation, a type of structural variation that is also informative for population genetic inference[89].

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Identifying past climate-associated declines

To detect possible climate-linked declines in Arctic charr, we first used LinkNe[37], a method that combines estimates of recombination rate with linkage disequilibrium information, to estimate historical effective population size (N_e) from 1900 to 2013, similar to studies that have examined declines in Atlantic salmon[59] and Atlantic cod[60]. This method was run using 968 SNPs on the array ~~with~~ that had corresponding linkage map information from ref. [64] ~~[62]~~. For each population, N_e was calculated using LinkNe, with bins of 0.05 Morgans, and including only SNPs with minor allele frequencies exceeding 0.05. We used recombination rate to bin N_e estimates by generation and calculated approximate years assuming generation times of four years. We then extracted climate and community biomass data for the North Atlantic from 1985 to 2013 from ref. [37], spanning a known cooling event that negatively impacted community composition and functional diversity in the region[37]. Climate index is a sum of multiple environmental time series and community biomass data derives from 30 demersal fish species[37]. We also included mean whole weight (kg) of Arctic charr from the Nain region of Labrador, one of the longest-

sampled commercial fisheries for charr in Canada[90], spanning the same time period. Additionally, we used abundance and mean weight of Arctic charr (summed across 12 age classes) before (1977–1984) and during (1990–1992) the decline to quantify the loss of biomass, translating to a loss of available protein for surrounding communities.

Reporting Summary

Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41558-020-00959-7.

Extended data is available for this paper at https://doi.org/10.1038/s41558-020-00959-7.

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Author contributions

K.K.S.L., P.V.R.S. and I.R.B. designed the study. K.K.S.L., T.K., S.J.L. and R.R.E.S. contributed to statistical analyses. P.V.R.S., J.B.D., P.B., S.J.D., A.M.M., C.M.N., M.M.F., J.S.L. and B.F.K. provided molecular data and metadata for the study. All authors discussed the findings. K.K.S.L. wrote the manuscript with contributions from all authors.

Data availability

Environmental, climate, community biomass, weight and abundance data were compiled from publicly available sources or other studies (https://doi.org/10.1098/rsos.170215 (ref. [37]), Dempson 1993, and Dempson 1995) ~~and these compiled data files are available at the following Dryad repository: https://doi.org/10.5061/dryad.8sf7m0ckd.~~ Genotype data are ~~also~~ available at: https://doi.org/10.5061/dryad.8sf7m0ckd.

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Code availability

~~R scripts are available at the Dryad repository: https://doi.org/10.5061/dryad.8sf7m0ckd.~~ No custom scripts were used in these analyses.

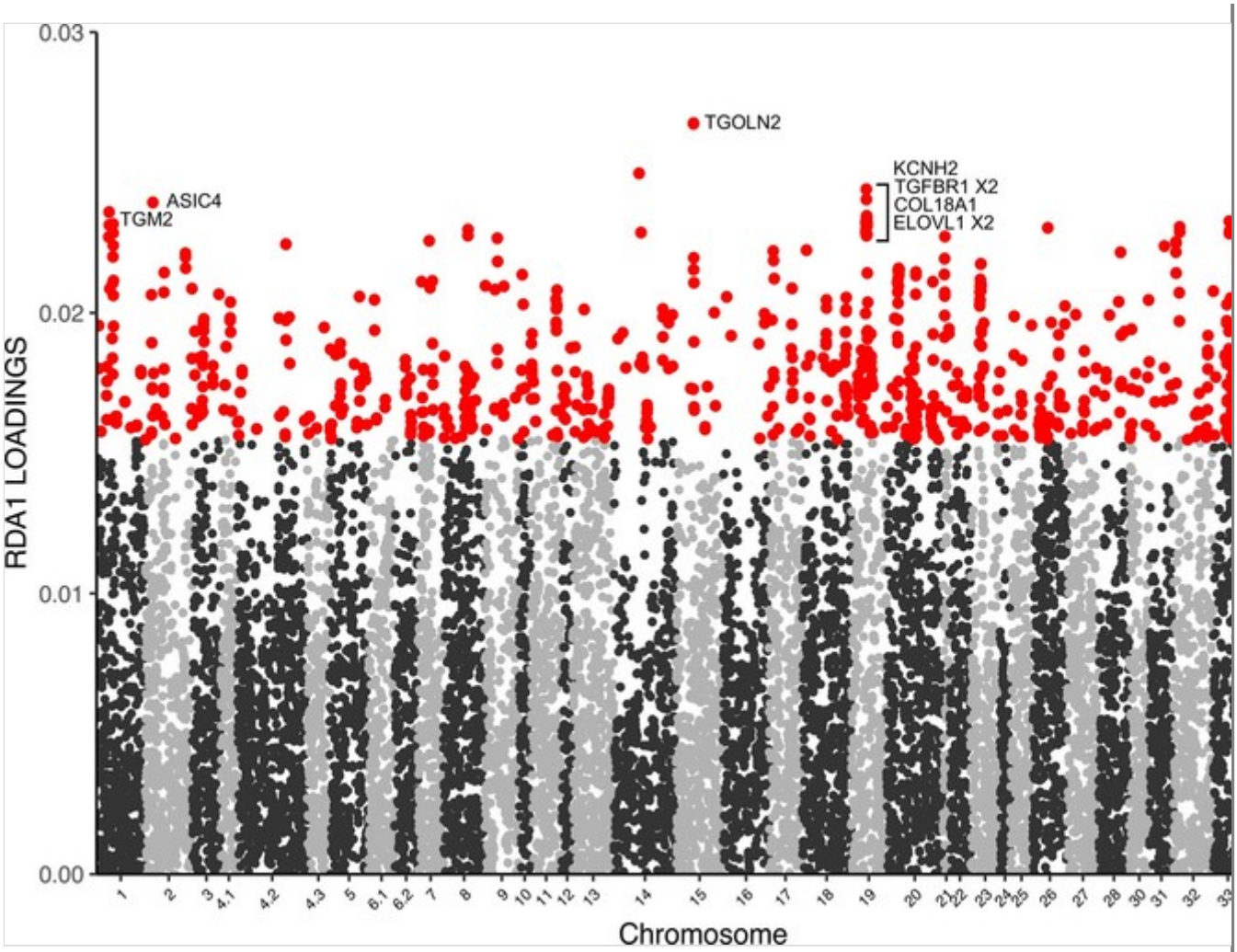
Competing interests The authors declare no competing interests.

Extended data

Extended Data Fig. 1

Absolute loadings for each SNP along the first canonical axis in an RDA.

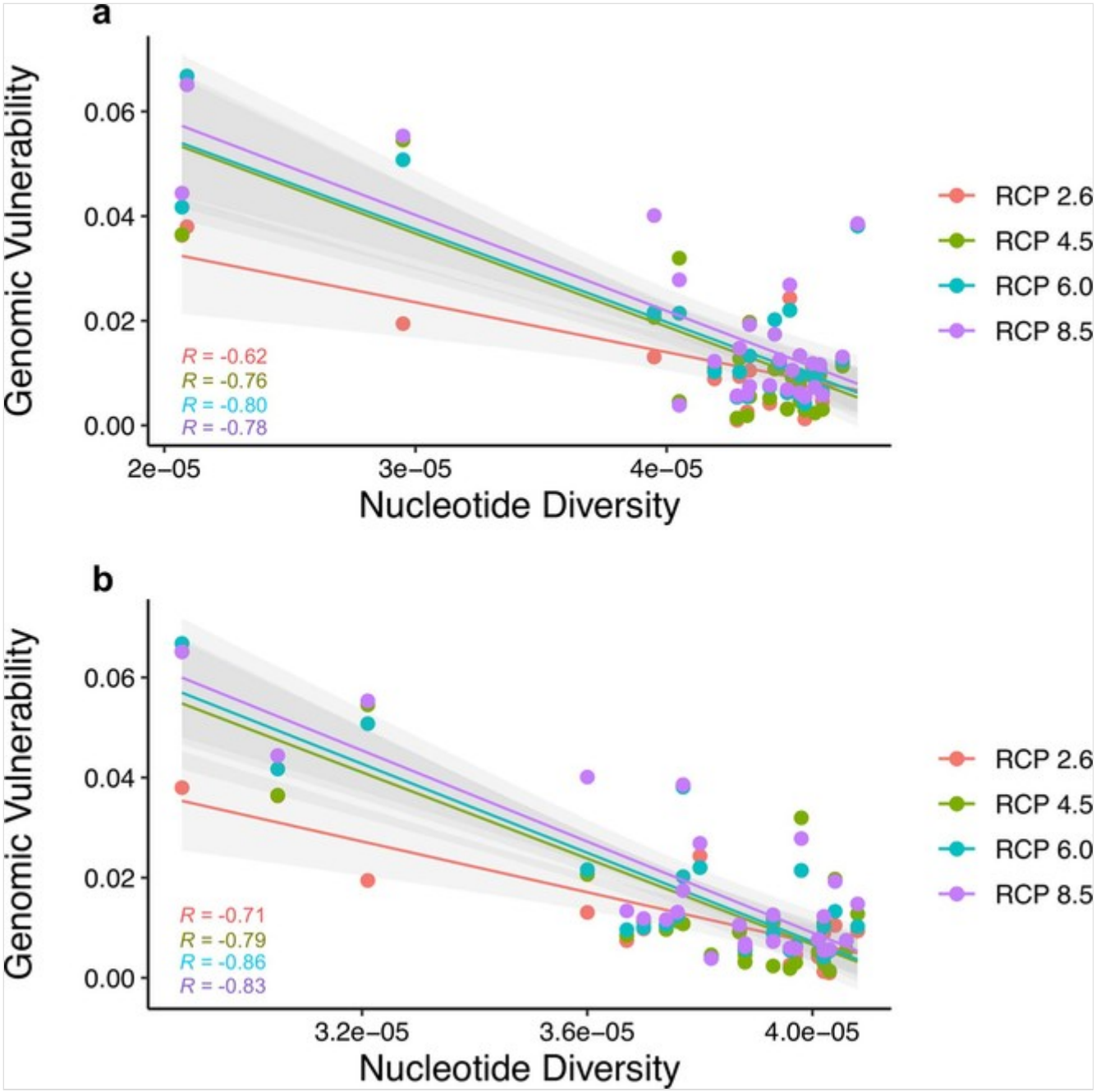
Absolute loadings for each SNP along the first canonical axis in an RDA with SNPs in the top 95th percentile treated as significant. Environment-associated SNPs are highlighted in red and genes located near top SNPs are labeled (ASIC4 = acid-sensing ion channel 4-like, COL18A1= collagen alpha-1(XVIII) chain, ELOVL1= elongation of very long chain fatty acids protein 1, KCNH2= potassium voltage-gated channel subfamily H member 2-like, PITPNB= phosphatidylinositol transfer protein beta isoform, TGFBR1= TGF-beta receptor type-1, TGM2= protein-glutamine gamma-glutamyltransferase 2, TGOLN2= trans-Golgi network integral membrane protein 2).



Extended Data Fig. 2

Genomic vulnerability is strongly negatively correlated with nucleotide diversity.

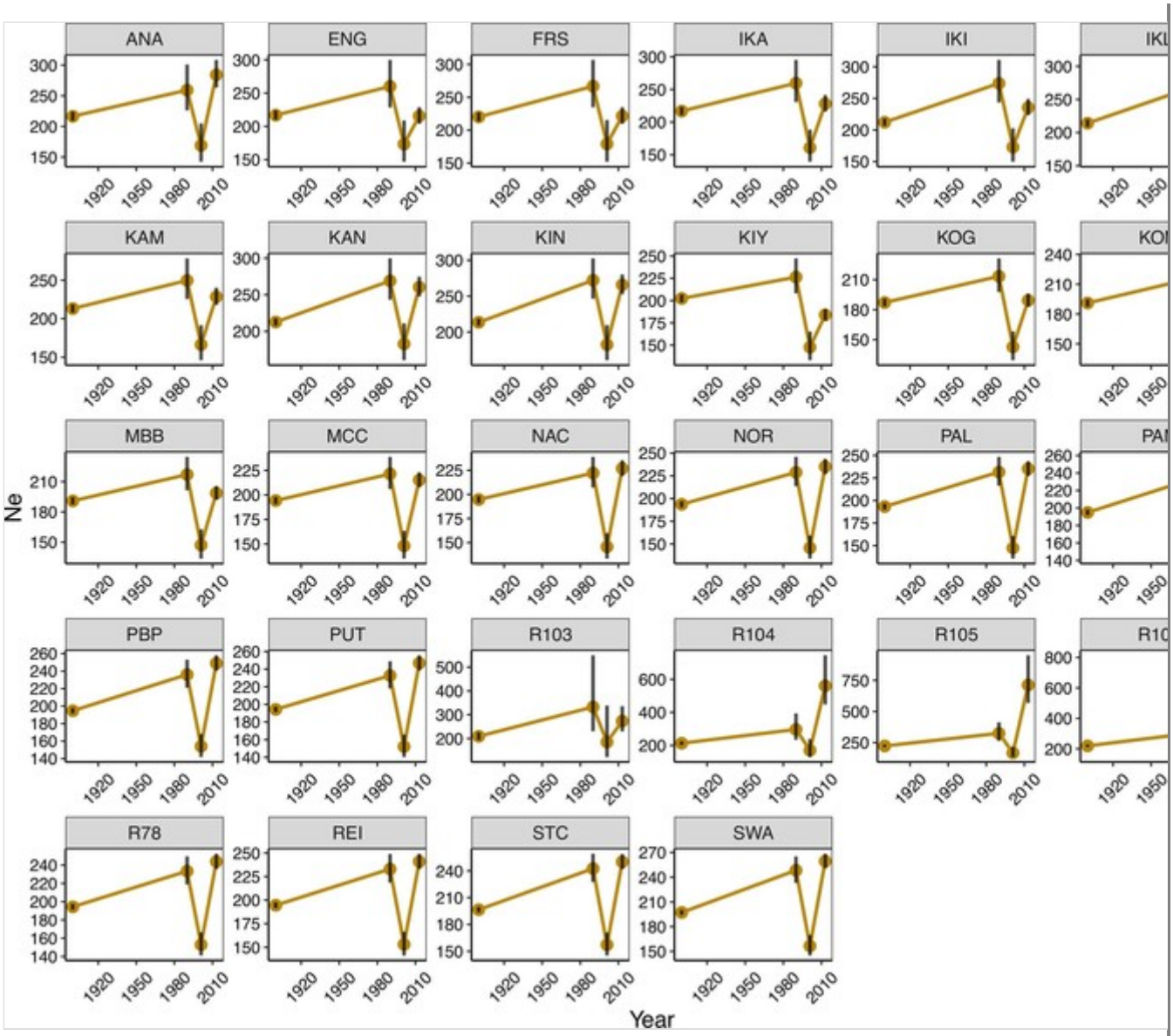
Genomic vulnerability is strongly negatively correlated with nucleotide diversity at **a** all 16,431 SNPs in this study and **b** 822 environment-associated SNPs under four different emissions scenarios.



Extended Data Fig. 3

Effective population size (*Ne*) estimates with confidence intervals.

Effective population size (*Ne*) estimates, representing number of individuals, for 28 populations of Arctic Charr. 95% confidence intervals appear in black and population codes appear in Supplementary Table 1.



Supplementary information

Supplementary Information Reporting Summary

Supplementary Figs. 1–5 and Tables 1–6.

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